Geodermatophilus sabuli sp. nov., a γ-radiation-resistant actinobacterium isolated from desert limestone

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A novel γ-radiation-resistant and Gram-staining-positive actinobacterium designated BMG 8133T was isolated from a limestone collected in the Sahara desert of Tunisia. The strain produced dry, pale-pink colonies with an optimum growth at 35–40 °C and pH 6.5–8.0. Chemotaxonomic and molecular characteristics of the isolate matched those described for members of the genus Geodermatophilus. The peptidoglycan contained meso-diaminopimelic acid as diagnostic diamino acid. The main polar lipids were phosphatidylcholine, diphosphatidylglycerol, phosphatidylinositol, phosphatidylethanolamine and one unspecified glycolipid. MK-9(H4) was the dominant menaquinone. Galactose and glucose were detected as diagnostic sugars. The major cellular fatty acids were branched-chain saturated acids iso-C16:0 and iso-C15:0. The DNA G+C content of the novel strain was 74.5 %. The 16S rRNA gene sequence showed highest sequence identity with Geodermatophilus ruber (98.3 %). Based on phenotypic results and 16S rRNA gene sequence analysis, strain BMG 8133T is proposed to represent a novel species, Geodermatophilus sabuli sp. nov. The type strain is BMG 8133T (DSM 46844T = CECT 8820T).

Members of actinobacterial species classified in the genus Geodermatophilus are best known for their resistance to adverse environmental conditions such as UV light, ionizing radiation, desiccation and heavy metals (Gtari et al., 2012; Montero-Calasanz et al., 2014a, 2015; Rainey et al., 2005). Some strains have also been reported to produce remarkably resistant enzymes, such as esterases (Essoussi et al., 2010; Jaouani et al., 2012; Normand et al., 2014b). The genus Geodermatophilus is grouped together with the genera Blastococcus and Modestobacter into the family Geodermatophilaceae (Normand, 2006; Zhi et al., 2009) in the order Geodermatophilales (Sen et al., 2014). The genus currently comprises 18 recognized species, mainly isolated from arid and hyperarid environments, such as sand and stone, although some have also been isolated from rhizospheric soils and lake sediments. Besides Geodermatophilus obscurus G-20T, which was isolated by Luedemann (1968) and the genome sequenced by Ivanova et al. (2010), 17 additional species with validly published names have recently been classified in the genus (Zhang et al., 2011; Nie et al., 2012; Jin et al., 2013; Qu et al., 2013; Bertazzo et al., 2014; Hezbri et al., 2015; Montero-Calasanz et al., 2015).

During the investigation of a dust microbial population in limestone grooves sampled from the Sahara desert of Tunisia located in Ong Jmal (34° 00’ 51” N 7° 53’ 39” E,
Tozeur), an actinobacterium strain designated BMG 8133T was isolated on Luedemann medium (DSMZ medium 877; Luedemann, 1968) by the dilution plate method. The purified strain was maintained on agar as well as stored at −80 °C in glycerol (35%, w/v) stocks and was further subjected to polyphasic characterization experiments. Colonies and general cultural characteristics were observed from culture growing at 37 °C for 15 days on different media: GYM Streptomyces medium (DSMZ medium 65), R2A medium (DSMZ medium 830), Luedemann medium (DSMZ medium 877), medium 5006, medium 5265 (ISP2), medium 5323 (ISP5, DSMZ medium 993) and 5322 (ISP7) (Shirling & Gottlieb, 1966). Cell morphology of strain BMG 8133T was determined from exponentially growing culture on GYM Streptomycetes medium at 37 °C using an optical microscope (Zeiss AxioScope A1) with ×100 magnification and phase-contrast illumination together with a field-emission scanning electron microscope (FE-SEM; Zeiss Merlin). Gram staining was carried out using the standard Gram reaction (Gram, 1884). The oxidation of carbon compounds was tested using GEN III Microplates in an Omnilog device (Biolog) in comparison with the reference strains: Geodermatophilus africanus DSM 45422T, Geodermatophilus amargosae DSM 46136T, Geodermatophilus arenarius DSM 45418T, Geodermatophilus dichtyosporus DSM 43161T, Geodermatophilus nigrescens DSM 45408T, Geodermatophilus normandii DSM 45417T, Geodermatophilus obscurus DSM 43160T, Geodermatophilus poikilotrophi DSM 44209T, Geodermatophilus ruber DSM 45317T, Geodermatophilus saharensis DSM 45423T, Geodermatophilus siccatus DSM 45419T, Geodermatophilus telluris DSM 45421T and Geodermatophilus zadiensis DSM 45416T in parallel assays. The GEN III Microplates were inoculated with cells suspended in a viscous inoculating fluid provided in parallel assays. The GEN III Microplates were inoculated with cells suspended in a viscous inoculating fluid provided for pH values from 4.0 to 12.5 (in increments of 0.5 pH units) on modified ISP2 medium (without agar) by adding NaOH or HCl, respectively, since the use of a buffer system inhibited growth of the strains. Degradation of specific substrates was examined using agar plates with various basal media: casein degradation was tested on plates containing milk powder (5% w/v), NaCl (0.5%) and agarose (1%); tyrosine degradation was determined as previously described by Gordon & Smith (1955) on plates containing peptone (0.5%), beef extract (0.3%), L-tyrosine (0.5%) and agarose (1.5%); xanthine and hypoxanthine decomposition (0.4%) were examined using the same basal medium; starch degradation was tested on plates containing nutrient broth (0.8%), starch (1%) and agarose (1.5%), then developed by flooding with 1% iodine solution. For all tests, a positive result was defined by the appearance of clear zones around the colonies. Whole-cell amino acids and sugars were prepared according to Lechevalier & Lechevalier (1970), followed by TLC analysis (Stanek & Roberts, 1974). Extraction of polar lipids was separated by two-dimensional TLC and identified according to protocol described by Innikin et al. (1984). Choline-containing lipids were also detected by spraying with Dragendorff’s reagent (Merck) (Tindall, 1990). Menaquinones were methanol-extracted from freeze-dried cell material (Collins et al., 1977) and analysed by HPLC (Kroppenstedt, 1982). The extraction and analysis of cellular fatty acids was carried out twice from four-day-old culture growing at 28 °C on GYM agar plates. Analysis was conducted using the Microbial Identification System (MIDI) Sherlock version 6.1 (method TSBA40, ACTIN6 database) as described by Sassar (1990). The composition of peptidoglycan hydrolysates (6 M HCl, 100 °C for 16 h) was examined by TLC as described by Schleifer & Kandler (1972). All chemotaxonomic analyses were conducted under standardized conditions with strain BMG 8133T and cultures of the same set of reference strains as listed in Table 1. The G+C content of the chromosomal DNA was determined by HPLC according to Mesbah et al. (1989). Genomic DNA extraction, PCR-mediated amplification of the 16S rRNA gene and purification of the PCR product was carried out as described by Rainey et al. (1996). The strain was identified using the 16S rRNA gene sequence on Ez-Taxon-e (Kim et al., 2012) and RDP-II servers (Maidak et al., 2001). Pairwise similarities were calculated as recommended by Meier-Kolthoff et al. (2013). Sequence analyses and phylogenetic reconstruction were performed using MEGA 6.0 (Tamura et al., 2013). The stability of relationships was assessed through bootstrap analysis (Felsenstein, 2005), by performing 1000 resamplings for the tree topology.

The tolerances of strains BMG 8133T and G. obscurus DSM 43160T (=G-20T), as a positive control (Gtari et al., 2012), to ionizing radiation were assayed using non-sporulating cultures grown at 37 °C for 5 days on Luedemann medium supplemented with tryptose (Difco) (Ishiguro & Wolfe, 1970). Bacterial cells were collected, washed twice with 0.9% NaCl, homogenized and subsequently

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Table 1. Phenotypic characteristics of BMG 8133<sup>T</sup> and members of closely related species

| Characteristic | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Colony colour on GYM | Pale pink | Light red, red | Light-orange, black | Black | Light red, black | Light red, brown | Light black | Light red | Black | Light red | Black | Light red | Black | Coral Pink | Black | Coral Pink | Light red, black | Moist |
| Colony surface on GYM | Dry | Moist | Moist | Dry | Moist | Moist | Moist | Moist | Dry | Moist | Dry | Moist | Dry | Moist | Dry | Moist | Moist |
| pH optimum | 6.5–8.0 | 7.0–7.5 | 6.0–9.5 | 6.5–8.0 | ND | 7.0 | 6.0–8.0 | 6.0–8.5 | 6.0–8.5 | 6.0–8.5 | 7.0 | 6.0–8.0 | 6.0–10.0 | 7.0 | 6.0–12.0 | 6.5–8.5 | 7.0–9.5 |
| Utilization of: | | | | | | | | | | | | | | | | | | | |
| Maltose | + | + | +/+ | + | + | + | + | + | + | + | + | + | + | −/+ | + | + | + | + |
| Cellobiose | + | + | +/+ | + | + | + | + | − | + | − | + | − | + | − | + | + | + | + |
| Turanose | − | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + | + | + |
| α-Lactose | − | + | +/+ | + | − | + | + | + | + | + | + | + | + | + | − | + | + | + |
| D-Mannose | − | − | + | + | + | + | + | + | + | − | + | + | + | + | + | − | + | + |
| D-Galactose | + | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| L-Rhamnose | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| Sodium lactate | − | + | +/+ | +/+ | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| D-Arabitol | − | − | +/+ | +/+ | + | + | + | + | + | + | + | + | + | + | + | + | + | + |
| D-Glucose | − | − | +/+ | +/+ | + | − | + | − | + | + | + | + | + | + | − | + | + | + |
| L-Lactose | − | − | +/− | + | − | − | + | + | + | + | + | + | + | + | − | + | + | + |
| L-Arginine | − | − | +/− | + | + | + | + | + | + | + | − | − | − | − | − | − | − | − |
| L-Glutamic acid | + | + | +/− | + | + | + | + | + | + | − | − | − | − | − | − | − | − | − |
| L-Histidine | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| Pectin | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| Methyl | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| Pyruvate | − | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| α-Lactate | +/− | + | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |
| D-Malic acid | + | − | + | + | + | + | + | + | + | + | + | + | + | + | + | − | + | + |

Strains: 1, BMG 8133<sup>T</sup>; 2, *Geodermatophilus ruber* DSM 45317<sup>T</sup> (Zhang et al., 2011); 3, *Geodermatophilus aquaeductus* DSM 46834<sup>T</sup> (Hezbri et al., 2015); 4, *Geodermatophilus dictyosporus* DSM 43161<sup>T</sup> (Montero-Calasanz et al., 2015); 5, *Geodermatophilus obscurus* DSM 43160<sup>T</sup> (Gtari et al., 2012; Luedemann, 1968; Normand et al., 2014a); 6, *Geodermatophilus nigrescens* DSM 45408<sup>T</sup> (Nie et al., 2012); 7, *Geodermatophilus arenarius* DSM 45418<sup>T</sup> (Montero-Calasanz et al., 2012); 8, *Geodermatophilus siccatus* DSM 45419<sup>T</sup> (Montero-Calasanz et al., 2013a); 9, *Geodermatophilus saharensis* DSM 45423<sup>T</sup> (Montero-Calasanz et al., 2013b); 10, *Geodermatophilus tzadiensis* DSM 45416<sup>T</sup> (Montero-Calasanz et al., 2013c); 11, *Geodermatophilus telluris* DSM 45421<sup>T</sup> (Montero-Calasanz et al., 2013d); 12, *Geodermatophilus soli* DSM 45416<sup>T</sup> (Montero-Calasanz et al., 2013c); 13, *Geodermatophilus africani* DSM 45422<sup>T</sup> (Montero-Calasanz et al., 2013e); 14, *Geodermatophilus terrae* DSM 45844<sup>T</sup> (Jin et al., 2013); 15, *Geodermatophilus. africanus* DSM 45422<sup>T</sup> (Montero-Calasanz et al., 2013f); 16, *Geodermatophilus taihuensis* DSM 45962<sup>T</sup> (Qu et al., 2013); 17, *Geodermatophilus amargosae* DSM 46136<sup>T</sup> (Montero-Calasanz et al., 2013b); 18, *Geodermatophilus sabuli* DSM 44526<sup>T</sup> (Bertazzo et al., 2014); 19, *Geodermatophilus poikilotroph* DSM 44209<sup>T</sup> (Montero-Calasanz et al., 2014a).

+, Positive; −, negative; +/-, ambiguous; ND, not determined. APL, unknown aminophospholipid; DPG, diphosphatidylglycerol; MK, menaquinones; PC, phosphatidylcholine; PE, phosphatidylethanolamine; PE-OH, hydroxy-phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PIM, phosphatidylinositol mannoside; PL, unknown phospholipid; PME, phosphatidyl-N-methylmethanolamine.
Table 1. cont.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
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<th>16</th>
<th>17</th>
<th>18</th>
<th>19</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predominant menaquinones*</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
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<td>MK-9(H₄), MK-9(H₃)</td>
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<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td>MK-9(H₄), MK-9(H₃)</td>
<td></td>
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<tr>
<td>Major fatty acids†</td>
<td>i-C₁₆ : 0, i-C₁₅ : 0, ai-C₁₇ : 0, ai-C₁₅ : 0, i-C₁₆ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
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<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
<td>i-C₁₅ : 0, i-C₁₆ : 0, i-C₁₇ : 0, i-H-C₁₆ : 1</td>
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<tr>
<td>DNA G+C content (mol%)</td>
<td>74.5</td>
<td>72.8</td>
<td>ND</td>
<td>75.3</td>
<td>73.9</td>
<td>75.1</td>
<td>75.9</td>
<td>77.9</td>
<td>75.2</td>
<td>75.4</td>
<td>74.1</td>
<td>74.4</td>
<td>75.5</td>
<td>73.2</td>
<td>73.0</td>
<td>75.4</td>
<td>74.4</td>
<td></td>
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<tr>
<td>Resistance to γ-radiation (LD₁₀, kGy)</td>
<td>6</td>
<td>8</td>
<td>ND</td>
<td>8.5</td>
<td>9</td>
<td>ND</td>
<td>ND</td>
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<td>ND</td>
<td>ND</td>
<td>ND</td>
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</table>

*Only components making up ≥5% peak area ratio are shown.
†Components are listed in decreasing order of quantity.
‡Only components making up ≥10% peak area ratio are shown.
resuspended in saline solution. Ionizing-radiation tolerance experiments were carried out according to a protocol outlined by Gtari et al. (2012). After a 2 week period, c.f.u. were counted and the survival fractions were calculated based on a non-irradiated control, using the R software packages ‘mgcv’ (Wood, 2014) and ‘lethal’ (Hofner, 2014), as previously described (Montero-Calasanz et al., 2014a).

Colonies of strain BMG 8133T were pale pink, irregular, multilocular and opaque with a dry surface and an irregular margin appearance similar to other members of the genus (Table 1). Cells of strain BMG 8133T were pleomorphic and Gram-staining-positive. Individual cells and cauliflower-like aggregates were observed, confirming reports by Ishiguro & Wolfe (1970) of synchronous morphogenesis on unspecific media and previous observations on other members of the genus Geodermatophilus (Montero-Calasanz et al., 2014b) (Fig. 1). Strain BMG 8133T grew well on GYM Streptomycyes, Luedemann, ISP2, ISP7 and 5006 media but not on R2A or ISP5 media. It tolerated a temperature range of 25–45 °C with an optimum at 35–40 °C. Growth occurred at 1–4 % NaCl, but not at 8 % NaCl, and at pH 6.5–10.5 with an optimal pH range of 6.5–8.0. Results from phenotype microarray analysis are shown as a heat map (see Fig. S1, available in the online Supplementary Material) in comparison with other reference type strains of the genus Geodermatophilus. A summary of selected differential phenotypic characteristics is presented in Table 1. Cell wall contents included meso-diaminopimelic acid (cell wall type III), which is consistent with other species of the genus Geodermatophilus (Hezbri et al., 2015; Lechevalier & Lechevalier, 1970; Montero-Calasanz et al., 2014a). The predominant menaquinone was MK-9(H4) at 82.9 %, in accordance with values reported for the family Geodermatophilaceae (Normand, 2006), but MK-9(H6) was also detected, at 10.0 %. The major fatty acids were the saturated branched-chain acids iso-C16 : 0 (37.3 ± 0.6 %) and iso-C15 : 0 (16.8 ± 1.0 %) complemented by anteiso-C15 : 0 (10.8 ± 0.4 %) and anteiso-C17 : 0 (10.7 ± 0.2 %). Phosphatidylcholine, diphostatidylglycerol, phosphatidylinositol, and phosphatidylethanolamine were the major phospholipids (see Fig. S2), constituting a similar pattern obtained in this study for other species of the genus Geodermatophilus (Table 1). Whole-cell sugar analysis revealed the presence of glucose and galactose as diagnostic sugars (Lechevalier & Lechevalier, 1970) complemented by traces of ribose and mannose. The DNA G+C content was 74.5 %. The almost complete (1367 bp) 16S rRNA gene sequence of strain BMG 8133T was determined. The 16S rRNA gene sequence supported affiliation to the genus Geodermatophilus, being mostly closely related to the type strain of G. ruber with 98.3 % sequence similarity. Meier-Kolthoff et al. (2013) reported an Actinobacteria-specific 16S rRNA threshold of 99.0 % with 1.0 % as maximum probability of error; this is assumed to correspond to DNA–DNA hybridization values above the required 70 % threshold recommended to assign a given strain to a novel species (Wayne et al. 1987). Thus, DNA–DNA hybridization with the type strain of G. ruber appear to be dispensable in designating strain BMG 8133T as the type strain of a novel member of the genus Geodermatophilus. Maximum-likelihood treeing placed strain BMG 8133T together with type strains of all species of the genus Geodermatophilus within the same phylogenetic group (Fig. 2).

Strain BMG 8133T exhibited a LD10 of 6 kGy (Fig. 3) that is considered lower than those of G. obscurus DSM 43160T and G. poikilotrophi, which are reported to be around 9 kGy (Montero-Calasanz et al., 2014a). However, the LD10 value of BMG 8133T is comparable to the model radioresistant bacterium Deinococcus radiodurans R1, which has a LD10 of 5 kGy (Battista et al., 1999).

Apart from the phylogenetic analysis based on 16S rRNA gene sequences, several phenotypic features support the distinctiveness of strain BMG 8133T from representatives of all other species of the genus Geodermatophilus (Table 1). Based on the phenotypic and genotypic data presented, we propose that strain BMG 8133T represents a novel species within the genus Geodermatophilus, for which the name Geodermatophilus sabuli sp. nov. is proposed.

**Description of Geodermatophilus sabuli sp. nov.**

Geodermatophilus sabuli (sa’bu.li. L. gen. neut. n. sabuli of sand, referring to the origin of isolation of the species).

The colonies are pale pink, irregular, multilocular with a dry surface. Cells are Gram-staining-positive, catalase-positive and oxidase-negative. Diffusible brown pigmentation is produced on ISP7 media (DSM medium 5322). Utilizes a wide range of carbon and nitrogen sources (Table 1).

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**Fig. 1.** Scanning electron micrograph of strain BMG 8133T culture grown for 7 days on GYM Streptomycyes medium and at 37 °C and showing circular, elliptical and germinated zoospores forming septated filaments. Bar, 2 μm.
Negative for aesculin degradation, the reduction of nitrate and denitrification, indole production and casein, tyrosine, starch, xanthine, gelatin and hypoxanthine degradation.

Tests for alkaline phosphatase and leucine arylamidase are positive, but those for valine arylamidase, β-galactosidase, α- and β-glucosidase, acid phosphatase, naphthol-AS-BI-phosphohydrolase, lipase (C14), cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, β-glucuronidase, N-acetyl-β-glucosaminidase, α-mannosidase, urease and α-fucosidase are negative. Cell growth occurs at 25–45°C and pH 6.5–10.5. The peptidoglycan in the cell wall contains meso-diaminopimelic acid as diamino acid, with galactose and glucose as diagnostic sugars. The predominant menaquinone is MK-9(H4). The main polar lipids are phosphatidylcholine, diphosphatidylglycerol, phosphatidyl-inositol, phosphatidylethanolamine and one unspecified glycolipid. Cellular fatty acids consist mainly of branched-chain saturated acids iso-C16:0 and iso-C15:0.

**Fig. 2.** Maximum-likelihood phylogenetic treeing based on 16S rRNA gene sequences and showing BMG 8133T phylogenetic position within the family Geodermatophilaceae. Only bootstrap values higher than 50% are shown above the branches. Bar, 0.01 substitutions per nucleotide position.

**Fig. 3.** Estimation of survival for strain BMG 8133T and G. obscurus strain DSM 43160T, used as positive control, following exposure to γ-radiation. The mean value of c.f.u. ml⁻¹ per strain is given, together with the LD₅₀ and LD₁₀ values in the upper panel of each figure. The γ-axis has a logarithmic scale.
The type strain is BMG 8133T (=DSM 46844T = CECT 8820T). The INSDC accession number for the 16S rRNA gene sequence of the type strain is LN626269.

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